A Conceptual Framework for Preventing the Spatial Dispersal of Invasive Plants

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Invasive plant species have adversely affected rangelands throughout the world and continue to invade previously uninfested lands at an alarming rate. Previous efforts have focused on eradication and control; however, recent efforts have recognized that preventing invasive plant species from infesting new areas is more cost-effective and efficient than trying to restore the system after it is infested. One of the major components of prevention is limiting the introduction of the invasive plant to uninfested areas. Guidelines to limit the introduction of invasive plants into new areas are usually general and not developed to address differences in dispersal vectors among invasive plants. To limit the dispersal of invasive plants, land managers need a framework that assists them in identifying major spatial dispersal vectors and management strategies based on those vectors. We propose an initial conceptual framework that integrates the ecology of invasive plant dispersal with prevention management. The framework identifies major potential vectors by incorporating invasive plant seed adaptations for dispersal through space and infestation locations relative to vector pathways. The framework then proposes management strategies designed to limit dispersal by those specific vectors. The framework also identifies areas where research could improve the effectiveness of dispersal-prevention strategies by providing additional management tools.

Key words: Invasion, weed prevention, vectors, weeds, spread.

Invasive plant species negatively impact rangelands throughout the world by displacing desirable species, altering ecological processes, reducing wildlife habitat, degrading systems, and decreasing productivity (DiTomaso 2000; Masters and Sheley 2001). Invasive plants are estimated to infest about 100 million ha in the United States (National Invasive Species Council 2001). Experts recognize invasive species are the second-most important threat to biodiversity after habitat destruction (Pimm and Gilpin 1989; Randall 1996; Whittenberg and Cock 2001). Furthermore, Wilcove et al. (1998) estimate invasive species have contributed to the placement of 35 to 46% of the plants and animals on the U.S. Federal Endangered Species List. In 1994, the impacts of invasive plant species in United States were estimated to be $13 billion per year (Westbrooks 1998). The amount of land infested by invasive plants is rapidly increasing (Westbrooks 1998) and, subsequently, the negative impacts of invasive plants are escalating.

Invasive plant management has traditionally focused on controlling invasive plants on already-infested rangelands, with less emphasis placed on preventing invasions. Often an invasion is recognized only after it has entered an explosive phase (Asher and Spurrier 1998). Unfortunately, by this stage eradication is not an option (Mack et al. 2000), and it is enormously expensive to control the increase of the invader (Huenneke 1996). This scenario leads to a reactive crisis-response approach to managing invasive plants (Hobbs and Humphries 1995; Jenkins 2002).

Given the complexity and persistence of invasive plants, a proactive approach focused on systematic prevention and early intervention would be more cost-effective and successful than the existing reactive approach (Peterson and Vieglasis 2001; Simberloff 2003; Zavaleta 2000). Prevention is an essential component of a successful invasive plant management program and often the most cost-effective management option (DiTomaso 2000; Sheley et al. 1996). The Office of Technology Assessment (1993) reported that targeted expenditures on prevention and early control provide solid economic returns where, on average, every dollar spent on early intervention prevented $17 in later expenses. The major components of invasive plant prevention include reducing the introduction of the invasive plant to uninfested areas (often through vector management), early detection and eradication of satellite patches, and increasing the resistance of desirable plant and soil communities to invasion (Sheley et al. 1999).

Information useful in developing comprehensive prevention programs for invasive plants is available but is scattered throughout the literature, making it difficult for managers to access, compile, and use the information to design effective prevention programs. Most discussions about prevention are little more than terse presentations of common sense lists of things to consider to prevent invasion and are only connected to the ecology of seed dispersal in some vaguely intuitive way (e.g. Sheley et al. 1999; Westbrooks et al. 1997). The need to create models based on the ecology of seed dispersal that enhance our ability to design comprehensive prevention programs is substantial and unmet. To limit the spread of invasive plants, land managers need a framework that assists them in identifying which vectors are major contributors to the spatial dispersal of specific invasive plants and proposes dispersal management strategies based on those major vectors. The purpose of this article is to provide an initial conceptual framework that integrates the ecology of invasive plant dispersal with prevention management that can be used as a component of a comprehensive prevention program. Ultimately, we believe linking these two concepts will enhance our ability to manage invasive plant species.

Spatial Seed Dispersal

Invasive plant seeds can meet many different fates (Figure 1). Invasive plant seeds can initially be shed in the immediate vicinity of their parent plant or population (pathway 1) or may be immediately dispersed (pathway 2) (Plummer and Keever 1963). Seeds that are shed next to their source may later be dispersed (pathway 4) or may remain at that location (pathway 3). Seeds may also be dispersed again (pathways 11 and 16). Some seed may also get destroyed in the dispersal process (pathways 7 and 12). Seed predators are

DOI: 10.1614/WS-06-161.1

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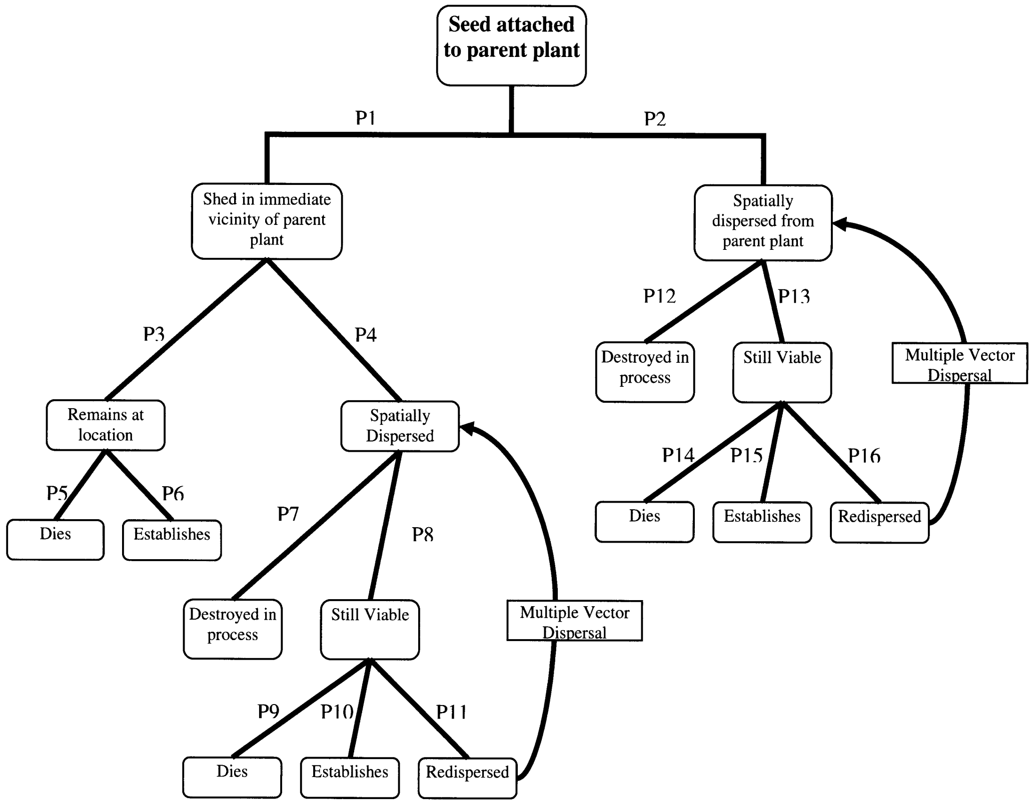

Figure 1. The potential fates of a seed. P1, pathway 1; P2, pathway 2; ...; P16, pathway 16.

an example of vectors that commonly disperse seeds shed in the immediate vicinity of their source and destroys some of the seeds in the process. Vander Wall (1994) reported that, although chipmunks (*Tamias amoenus* Allen) were consumers of bitterbrush[1] [*Purshia tridentata* (Pursh) DC.] seeds, they also dispersed seeds by forming caches.

Managing the fate of invasive plant seeds can greatly improve prevention success. For successful prevention of new infestations, management needs to limit the number of seeds following the pathways to successful establishment at previously uninfested locations. Creating any break or diversion in the pathways before establishment will reduce the likelihood of new invasions. Preventing dispersal of invasive plant seeds (pathway 2 and 4) has long been suggested for preventing new infestations of invasive plants, but prevention strategies are too general and not developed to account for dispersal differences among invasive plant species (e.g., Clark 2003).

Invasive plants encroach into uninfested rangeland by various vectors. Common vectors for transporting invasive plants include humans, vehicles, wind, water, insects, and animals. Some invasive plants also have mechanisms for self-propelled dispersal. The distance and quantity of seeds dispersed depend on the vector and invasive plant characteristics. Some invasive plants possess characteristics that increase the likelihood of their transport by specific vectors. In a review of other manuscripts, Sorensen (1986) reported that most adhesive seeds adhere to animals by barbs, hooks, or viscid outgrowths. An individual seed also can be dispersed more than once by multiple vectors. For example, in a Costa Rican forest, ants move a high percentage of seeds from bird defecations to their nest (Levey and Byrne, 1993). Specific invasive plants have vectors that are more important than other vectors to their dispersal. For example, western juniper (*Juniperus occidentalis* Hook.) seed dispersal occurs through overland water flow and animal transport; however, birds are the most important vector for juniper dispersal (Gabrielson and Jewett 1940; Maser and Gashwiler 1978). Prevention would be improved by understanding the relative importance of different vectors to the dispersal of specific invasive plants and using this knowledge to concentrate efforts where they would be most effective at limiting the spread of those invasive plants. Management strategies may differ depending on dispersal vectors.

Our model outlines plant adaptations for dispersal, infestation locations, and potential vectors that can be used as a framework for identifying important vectors to the dispersal of an invasive plant species or groups of invasive plants with similar seed traits and infestation locations. The framework also incorporates possible management strategies to limit specific vector transport of invasive plants and identifies where more research into creating additional management strategies would be valuable. Prevention efforts could then be improved by strategically inserting barriers to dispersal where they would be most effective at preventing new infestations.

Framework for Identifying Spatial Seed Dispersal Vectors

By identifying vectors that are major dispersers of an invasive plant species, management can more effectively

[1] Examples of plant dispersal were not limited to invasive plant species. Studies of native plant dispersal provide valuable information about dispersal mechanisms and interactions.

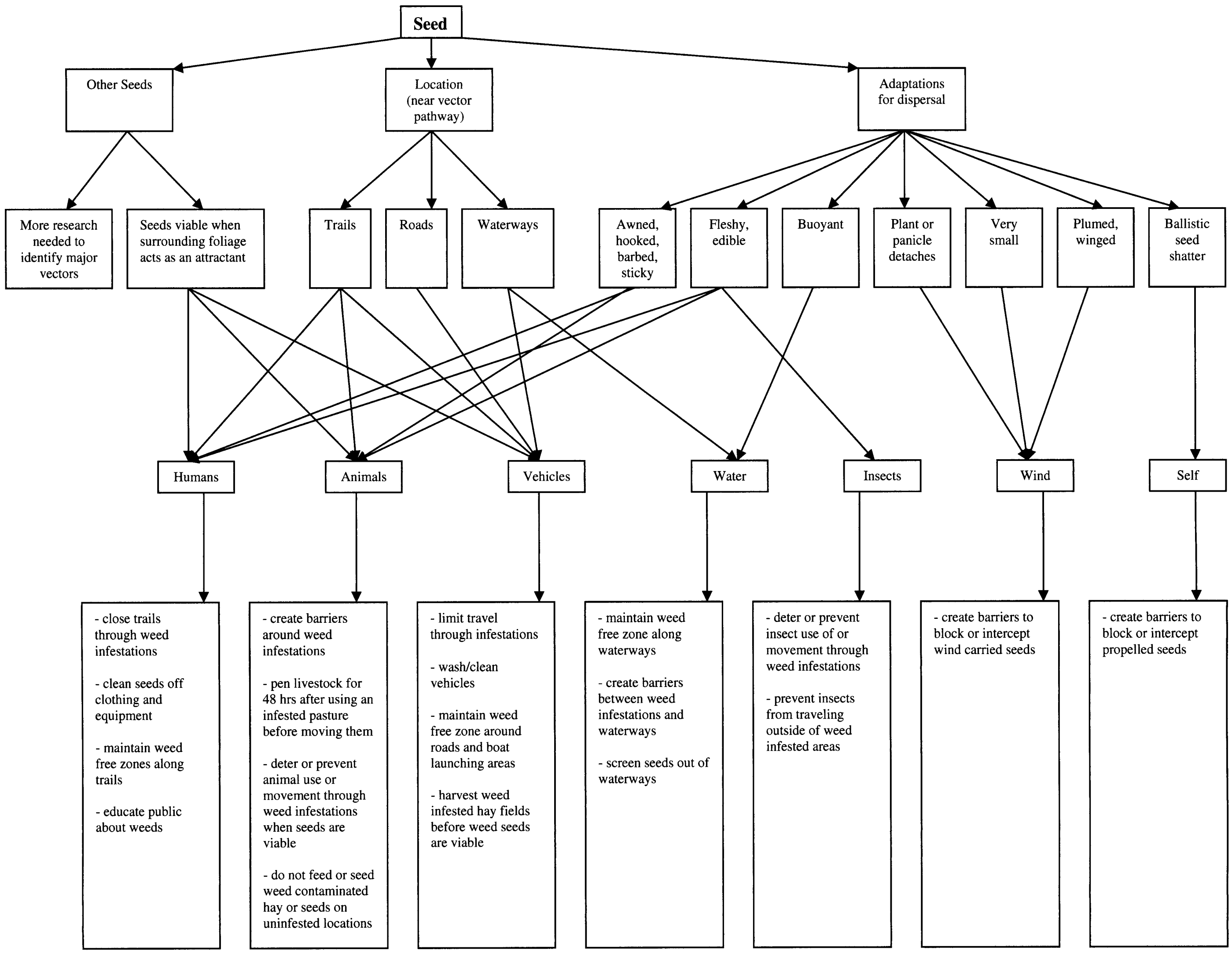

Figure 2. Depiction of the conceptual framework to identify which vectors are potential major spatial dispersers of an invasive plant species and to proposed dispersal management strategies.

prevent invasive plants from infesting new areas. Comprehensive prevention of invasive species includes identifying and managing major vectors (Ruiz and Carlton 2003; Wittenberg and Cock 2001). Management strategies could be developed that focus on creating barriers to limit dispersal by the key vectors of an invasive plant. To maximize efficiency, these plans would focus on the most important vectors.

Our framework for identifying which vectors are potentially the most important dispersers of a specific invasive plant is based on the morphology of the invasive plant, especially the seeds, and the location of infestations relative to vector pathways (Figure 2). Invasive plant species are grouped by seed traits and infestation locations in the framework to simplify management strategies. The framework also suggests management strategies for specific vectors and can be used to strategically search for satellite populations. By identifying likely vectors, searching for new infestations can be strategically conducted along those vector pathways. This framework incorporates previously-published literature that identified traits that facilitate specific vector transport.

Characteristics that Promote Specific Vector Dispersal

Attachment. Seeds with awned, hooked, sticky, or barbed appendages are likely to be transported by animals or humans. These seed structures adhere to animal's coats or people's clothing (Sorensen 1986). For example, hares (*Lepus capensis* L.) mainly transported hooked, barbed, or sticky seeds in their coats (Agnew and Flux 1970). Hooks, barbs, and awns increase the retention time, resulting in humans and animals being important vectors to dispersal of seeds with these adaptations (Shmida and Ellner 1983). Adhesion to people has the potential to result in long distance dispersal of invasive plants (Cousens and Mortimer 1995). Preventing dispersal of invasive plants with seeds with awns, hooks, or barbs should focus on limiting animal and human contact with the invasive plant when the seeds are mature.

Attractant. Seeds surrounded by a fleshy fruit or are edible can be transported by animals, humans, or insects. Animals, humans, and insects are attracted to the seed or the fleshy fruit as a food source. Some of these animals hoard seeds in caches, whereas others immediately ingest the seeds. Chipmunks and other rodents often cache seeds (Vander Wall 1994), whereas ungulates often ingest acacia (*Acacia* P. Mill.) and mesquite (*Prosopis* L.) seed pods while the seeds are still inside (Brown and Archer 1987; Miller 1996). Humans have dispersed edible seeds or seeds surrounded by fleshy fruits around the world. Birds have also been shown to be major vectors of seeds surrounded by fleshy fruit or edible seeds. For example, European starlings (*Sturnus vulgaris* L.) dispersed Russian olive (*Elaeagnus angustifolia* L.) seeds by ingesting its fruit (Kindschy 1998). Fish have also been shown to be important seed dispersers of some plant species with edible seeds or seed surrounded by edible flesh (Gottsberger 1978). Insects, such as ants, can also disperse seeds (Fedriani et al. 2004; La Tourrette et al. 1971; Roberts and Heithaus 1986).

Seeds that mature when surrounding foliage attracts consumers can also be transported by humans and animals. When humans harvest crop fields, any invasive species that has mature seeds intermixed with the crop can then be dispersed by the machinery harvesting and transporting the crop. The seeds of many plant species are dispersed by grazing animals that consume the seeds along with foliage (Janzen 1984). Vellend et al. (2003) reported that whitetail deer (*Odocoileus virginianus* Zimm.) ingest seeds of white trillium [*Trillium grandiflorum* (Michx.) Salisb.] while consuming foliage and dispersed those seeds occasionally > 3 km.

Limiting dispersal of invasive plants that attract or are surrounded by forage that attracts animals and humans could be improved with more research, but there are some tools available. Creating physical barriers can be an effective tool to prevent dispersal by some animals and humans. Adjusting when crops are harvested or forage is used can limit dispersal of invasive plants. Although not always practical, deterring or limiting use of infested areas by wild animals may be needed to reduce dispersal of some invasive plants.

Aerodynamic Properties. Many invasive plant species have adaptations that enhance their ability to be transported by wind. Plumed or winded appendages on seeds facilitate wind dispersal (Burrows 1986). For example, plumed camphorweed [*Heterotheca subaxillaris* (Lam.) Britt. & Rusby] seeds were wind-dispersed, whereas nonplumed seeds fell almost vertically to the ground (Plummer and Keever 1963). Whole plants or their panicles may disarticulate (break off) with the seeds still attached and then also be wind dispersed. Tumbleweeds break off at the stem allowing the entire aboveground portion to be dispersed by wind (Cousens and Mortimer 1995; Howe and Smallwood 1982). Grass panicles that disarticulate can be blown considerable distances along the ground, and maximum dispersal may be in the kilometers (Cousens and Mortimer 1995). Small seeds may also be wind dispersed because decreased weight to surface area (wing-load) increases wind dispersal distance (Augspurger and Franson 1987). More research is needed to advance our abilities to limit wind dispersal of seeds. However, seeding or promoting tall vegetation around infestations may limit dispersal by reducing wind velocities and physically intercepting seeds or structures (with seeds still attached) transported by wind.

Buoyancy. Buoyant seeds have the potential to be water dispersed. For example, crimsoneyed rosemallow (*Hibiscus moscheutos* L.) (Kudoh and Whigham, 2001) and flowering ash (*Fraxinus ornus* L.) (Thebaud and Debussche 1991) have buoyant seeds that are water dispersed. Some seeds can float for long periods, thus potentially increasing the distance they can be dispersed. Bald cypress [*Taxodium distichum* (L.) L.C. Rich.] and water tupelo (*Nyssa aquatica* L.) seeds can float for 2 to 3 mo (Schneider and Sharitz 1988), and rough cockleburr (*Xanthium occidentale* Bertol.) fruits can float for 30 d (Hocking and Liddle 1986). Fruits or other structures containing seeds that are buoyant may also be dispersed by water (Cousens and Mortimer 1995). Small seeds may also be water dispersed because of the small amount of energy required to transport them. Management of water-dispersed invasive plants can focus on keeping the seed out the water, removing seeds from the water, or preventing the seed from traveling from the water to a safe site while its still viable.

Self-Propelled. Invasive plants may have mechanisms for self-propelled dispersal of their seeds. The seeds of some plants are projected several meters (Beattie and Lyons 1975; Riley 1930). Others have explosive dehiscence that disperses seeds (Cousens and Mortimer 1995). For example, leafy spurge (*Euphorbia esula* L.) capsules erupt and project seeds during periods of high temperatures and low humidity (Selleck et al. 1962). Ballistic dispersal is often limited in its contribution to geographical spread of species but can be important to the localized expansion (Cousens and Mortimer 1995). Reducing ballistic dispersal would be similar to limiting wind dispersal. Feasible methods to reduce ballistic dispersal are generally lacking. However, promoting tall vegetation around self-dispersed invasive plants may reduce dispersal of the species by intercepting self-propelled seeds, and creating barriers of unsuitable habitat around infestations may prevent expansion beyond the patch.

Location. Invasive plants located near a vector pathway, such as a road, trail, or waterway, increase their chances of being dispersed by the vector using that pathway. For example, camphorweed seeds were found in the radiator and air filter of an automobile driven on a road adjacent to a camphorweed-infested area (Plummer and Keever 1963). Seeds can accidentally stick to the feet of animals (Darwin 1859), thus seeds without attachment or attractant adaptations may be transported in large numbers by animals if they are adjacent to an area of high animal traffic. Proximity to waterways greatly increases the likelihood of water dispersal. For example, wind dispersal appendages, such as plumes and wings, would aid water dispersal by increasing buoyancy (Cousens and Mortimer 1995). However, when water currents are strong, heavy, nonbuoyant seeds can also be water dispersed. Identification of vector pathways is critical to developing an effective plan to limit invasive plant dispersal. Management can then be tailored to limit invasive plant dispersal along specific vector pathways. For example, remote roads or hiking trails that dissect an invasive plant infestation can be closed or rerouted to limit vehicle and human transport of seeds. Management of roads or trails that cannot be closed or rerouted could focus on creating an invasive plant free-zone between the edge of the road or trail and infestation.

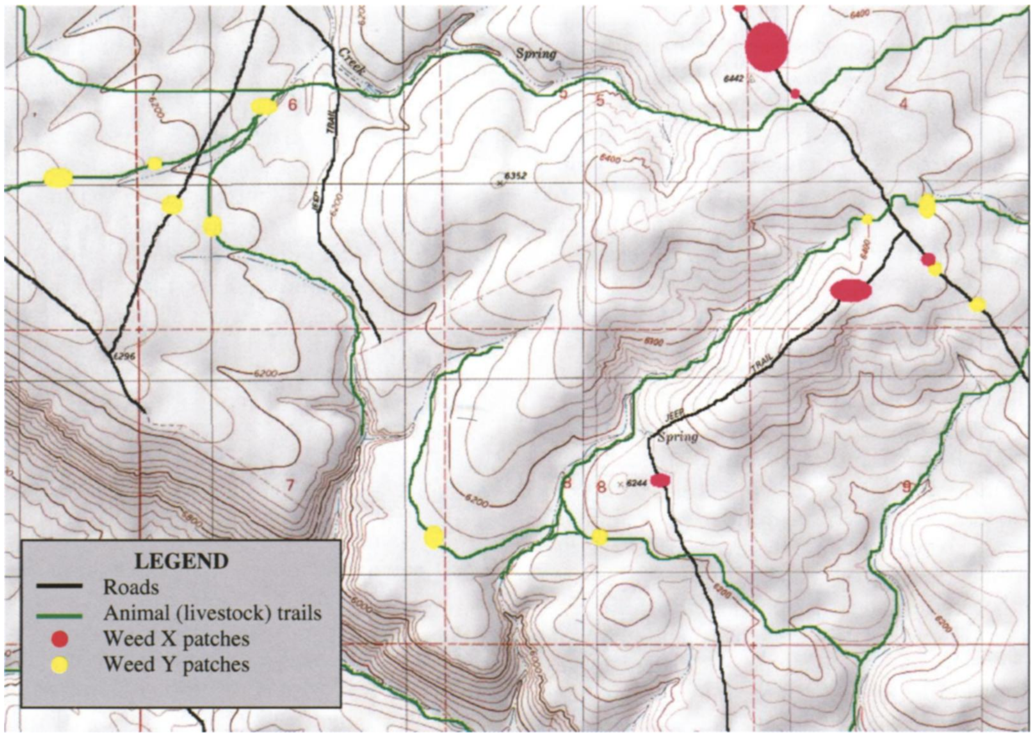

Figure 3. A map of a theoretical rangeland with weed X and weed Y infestations.

Multiple-Vector Dispersal

Though commonly not considered in managing invasive plants, multiple-vector dispersal can be an important determinant of the spread of invasive plants. Multiple-vector dispersal has been reported from insects transporting seeds already dispersed by animals (Kaufmann et al. 1991; Levey and Byrne 1993; Roberts and Heithaus 1986; Wicklow et al. 1984), animals redispersing insect-dispersed seeds (Fedriani et al. 2004; La Tourrette et al. 1971), animals dispersing seeds that other animals have already transported (Janzen 1982; Vander Wall 1994), wind interacting with animals or vehicles to disperse seeds (Plummer and Keever 1963; Vander Wall 1992), and wind and water dispersing the same seeds (Cousens and Mortimer 1995). Multiple-vector transport can greatly increase the maximum dispersal distance. After Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) seeds were wind dispersed, they were moved by rodents about three times farther at one site and five times farther at another site (Vander Wall 1992). Managing multiple vector dispersal seems daunting, but identifying potential secondary-transport vectors allows for more effective management. Once potential secondary vectors are recognized, they can be managed as if they were the primary vector or management can focus on breaking the linkage between the vectors. If secondary vectors require the seed to be dispersed initially by the first vector, reducing initial dispersal would also limit secondary dispersal.

Applying the Framework

The characteristics of the invasive plant species and infestation locations relative to vector pathways are incorporated into the framework (Figure 2) to determine the potential major vector or vectors. Once the major vectors are identified by the framework, invasive plant managers can use the framework to identify management strategies that would limit dispersal. At this stage, land managers use their knowledge of the situation to select, from the identified strategies, the best-suited management actions to meet their objectives. The framework allows managers to prioritize efforts to limit dispersal by ranking vectors according to their importance in the dispersal of the area's invasive plants and the effectiveness and feasibility of different management strategies. As new management strategies are developed or new invasive plants become a concern, they can be incorporated into the framework. This strategy allows the development of a comprehensive plan to limit dispersal of and/or manage invasive plants.

Although using the framework will improve management by focusing on the major vectors of specific invasive plants, random dispersal will still occur. For example, although hares mainly transported seeds with adhesive properties, they did infrequently transport some seeds without these adaptations (Agnew and Flux 1970). The framework will improve management plans to limit dispersal of invasive plants, but early detection and eradication of satellite patches and promoting resistance of plant communities to invasions will still be an important component of an effective prevention program. The framework can also be used to identify areas, based on major vectors, where strategic searching for satellite patches would be more effective.

Example of Applying the Framework

To demonstrate how to apply the framework, we analyze a theoretical situation where land managers are trying to limit invasive plant dispersal on a semiarid rangeland. Two invasive plants are a major concern on this rangeland (Figure 3). The rangeland is used for livestock grazing and recreation, and the management objective is to continue both of these uses. Livestock graze this area from late summer to early fall, and recreation mainly consists of motorized travel along the dirt roads during the summer and fall. Wildlife numbers, especially big game animals, are low in this area. Weed Y is an aggressive annual species with seeds that have barbed appendages. Seeds mature in late summer. Weed X is a biannual to short-live perennial species that has no evident adaptations for spatial dispersal. Weed X seeds mature from mid to late summer.

Incorporating the seed characteristics of the two invasive plants into the framework immediately reveals animals and humans are potential major vectors of weed Y; however, weed X does not have evident adaptations for dispersal. Examining the locations of weed X reveals that its infestations occur along roads (Figure 3). Incorporating this information into the framework reveals that vehicles, including possibly road maintenance equipment, are probably the major vector of weed X. Evaluating locations of weed Y suggests vehicles and animals are its major vectors because weed Y infestations are located near roads and animal trails. The framework has identified vehicles as a likely major vector of weed X, and vehicles, animals, and humans as potential major vectors of weed Y. Our knowledge that recreation is mainly limited to travel on roads suggest that humans, at least at this time, are not as potentially important vector as animals or vehicles for dispersal of weed Y on this rangeland. This area has low wildlife numbers and is used by livestock during seed maturity, which suggests livestock are probably the major animal vector of weed Y on this rangeland. The framework then provides possible management options to limit the dispersal of weed X and weed Y. To select the best management strategies, land managers evaluate the possible management strategies compatible with their objective to continue using the rangeland for recreation and livestock production. To limit vehicle dispersal of weed Y and weed X, land managers decided to create and maintain invasive plant–free zones between the roads and infestations. To reduce animal dispersal of weed Y, land managers change the livestock season of use to late spring to early summer. Changing the season of use results in livestock removal from the rangeland before weed Y seeds are mature. Other management strategies proposed by the framework could have been selected, but these strategies fit best with the management's objectives and resource availability.

Research Needed

The prevention of new invasive plant infestations could be improved by developing more effective tools for limiting dispersal of invasive plants. Identifying the major vectors that disperse an invasive plant and then developing strategies to reduce the dispersal effectiveness of those vectors will be critical to limiting new infestations. Our framework can be used to identify vectors that are major contributors to the dispersal of specific invasive plants; subsequent research efforts could focus on management strategies to limit dispersal by those vectors. For example, efficient management strategies to limit wind dispersal of invasive plants species are needed. The framework can also be used to identify invasive plant species that need to be analyzed more closely to identify the vectors that are major contributors to their dispersal.

Research can also improve invasive plant management by providing actual percentages or numbers of viable invasive plant seeds dispersed by specific vectors and testing the effectiveness of different management strategies on reducing those quantities. With the incorporation of dispersal amounts into the framework and effects of different management strategies, the effectiveness of different dispersal barriers at limiting dispersal of specific invasive plants could be predicted.

Summary

The framework described in this article conceptually links the invasive plant species characteristics and infestation locations with their modes of dispersal and provides management strategies based on those characteristics. Land managers can use the framework as a tool to guide efforts to limit dispersal of invasive plant seeds. Greater efficiency can be achieved using the framework because dispersal prevention plans can concentrate on the major dispersers of invasive plant species. Because strategies to limit the dispersal of invasive plant species have not been well developed, the suggested methods to reduce dispersal may be impractical in some situations, especially on a large scale. The framework also directs research toward developing procedures to prevent dispersal by specific vectors and quantifying the importance of different vectors to the dispersal of certain invasive plants.

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Received September 4, 2006, and approved December 4, 2006.